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MULTIPLE ALLELOMORPHS IN MICE

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SOME breeding experiments with mice that I have been carrying on during the last two years have shown that yellow, gray gray-belly, gray white-belly and black are allelomorphs. To this series a fifth allelomorph may possibly be added which for the present may be called new gray. This quadruple (or quintuple) system of allelomorphs fulfils the conditions of a multiple series in that only two of the allelomorphs can exist at the same time in any individual. In other words, a mouse may be pure for any of these genes (except for yellow, in which the pure form is not viable), or a mouse may be heterozygous in any two of the genes, but never in more than two. The evidence that establishes this series of allelomorphs may be briefly stated as follows:

In 1911, I pointed out that if yellow mice (producing yellow and chocolates) are bred to agoutis (grays), and their yellow offspring mated, they should produce not only yellow and agoutis (as they did) but some chocolates (or blacks) also; but no chocolates appeared. I stated that the results obtained were explicable if yellow and agouti are allelomorphs.[1]

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[1] The discussion in the same paper of the presence of chocolate yellow and black bars in the ticked hair in relation to the occurrence of chocolate, yellow and black color in domesticated races may only confuse the ontogenetic production of characters with the gametic inheritance of factors. The

Sturtevant (1912) showed that the results are also consistent with the hypothesis that there is close or complete linkage (genetic coupling) between yellow and agouti. In principle this is the same as saying that when yellow and agouti enter from different sides (mother and father) they separate in gametogenesis, or in other words they "repel" each other and behave, as I said, like allelomorphs.

The numerical results would be the same whether yellow and agouti are treated as though completely linked or whether they are treated as allelomorphic. What I had vaguely seen in my 1911 paper was clearly explained in the following year by Sturtevant's treatment of the same data, to which he added that of Little and Miss Durham.

Sturtevant showed, from an analysis of Miss Durham's results, in which she used ordinary gray (gray "gray-belly") mice, that her results are consistent with the hypothesis of absolute linkage, or, on my interpretation, with the hypothesis of allelomorphism. Sturtevant's conclusions were promptly contradicted by C. C. Little on the evidence furnished by some of his earlier experiments, in which he obtained yellow, grays and black (or chocolates) in offspring from yellow to black (or chocolates). Such a result would be inconsistent with Sturtevant's hypothesis. Little also appealed to certain experiments of Miss Durham, in which, he stated, results like his own are given. Since Little has been unable to get again his former results, but has obtained evidence in favor of Sturtevant's view, and since it is clear that he misunderstood Miss Durham's evidence, his contradiction ceases to have any weight.

factorial hypothesis relates to those differentials that serve to separate different types in inheritance and is not concerned with the problem as to how those differentials produce their effects. Breeding experiments show that gray differs from black by one differential, from yellow by another, and from cinnamon by a third. So far as Mendelian segregation of these differential genes is concerned it is of no consequence that the gray hair is made up of a black, a yellow, and a chocolate band.

After the publication of my own and of Sturtevant's paper I set to work to obtain crucial evidence in favor of, or opposed to, the view that yellow and gray are allelomorphic. Little, also, it appears, has carried out some new experiments which he has recently published, with the results just stated. My own data have been ready for some time, but I have withheld them in order to get a sufficient body of evidence to make the case convincing, especially in the light of the possibility that the crossing over might occur in one sex and not in the other. For, if no crossing over occurred in the male, there might be crossing over in the other sex, which would not reveal itself unless the experiments were deliberately planned so that both sexes are tested. This consideration seems to have been overlooked by Little, for he has omitted in his confirmatory paper to give the sexes of the animals used. Without a knowledge of this relation even his confirmation fails to confirm (as he supposes) the view that he formerly combated.

Since Miss Durham worked with common gray and I with gray white-belly, and both are "repelled" by yellow, *i. e.,* both are allelomorphs of yellow, it follows that these two grays are also allelomorphic to each other.

The evidence that black belongs to the same series of allelomorphs is obtained in the following way: If a given yellow is mated to black, and yellow and gray offspring are obtained, and if then the yellow offspring are mated to black again and now give yellow and black only, the proof is furnished; for in the first mating yellow and agouti have repelled each other, and the yellow-bearing gametes have united with the black gametes of the other sex to give the yellow offspring. The second mating shows that black is now repelled in turn by yellow and is therefore allelomorphic.

This may be illustrated in the following way: Let $B^Y =$ yellow, $b =$ black and $B =$ gray. These three factors may be treated as allelomorphs, then:

Yellow B^YB by black bb.

Gametes of P_1 yellow B^Y–B.
Gametes of P_1 black b–b.

F_1 B^Yb = yellow.
Bb = gray.

Gametes of F_1 yellow B^Y–b.
Gametes of pure black b–b.

F_2 B^Yb = yellow.
bb = black.

But if yellow and black and gray are not allelomorphic the same matings should give the following results:

Y' = yellow. y' = not yellow. b = black. B = "gray" (not black).

Yellow $Y'y'BB$ by black $y'y'bb$.

Gametes of P_1 yellow $Y'B$–$y'B$.
Gametes of P_1 pure black $y'b$–$y'b$.

F_1 $Y'B\ y'b$ = yellow.
$y'B\ y'b$ = gray.

Gametes of F_1 yellow $Y'b$–$Y'B$–$y'b$–$y'B$.
Gametes of pure black $y'b$–$y'b$.

F_2 $Y'b\ y'b$ = yellow.
$Y'B\ y'b$ = yellow.
$y'b\ y'b$ = black.
$y'B\ y'b$ = gray.

On the second assumption yellow, gray and black should appear in the back cross. The former and not the latter view is therefore consistent with the actual results.

THE SYMBOLS EMPLOYED

It is, of course, a matter of secondary importance what system of symbols is followed. The requirements are simplicity, consistency and suggestiveness, but one can not always arrange to have all three at the same time. The simplest scheme, for a system of allelomorphs like these, would be to have some common letter to indicate their relation and an exponent to suggest the different characters for which each stands. If we take the symbol b (black) for the common letter, and use capitals for dominance, the allelomorphs will be:

b = black.
B^G = gray gray belly.
B^W = gray white belly.
B^Y = yellow.

If one preferred to take Y (yellow) as the common letter the series would be y'^b, y'^g, y'^W, Y'; or, if one preferred to take *G* (gray), as the common letter, the series would be g^b, g^W, G, g^Y. On the whole the first series seems to me somewhat preferable.

The factor for cinnamon is entirely independent in heredity of the preceding series of allelomorphs. This factor may be represented by *ci* and its normal allelomorph by *Ci*. The formula for the wild gray would then be *Ci Ci,* and that for cinnamon would be *ci ci*. Black would be *b b,* and the double recessive cinnamon black (or chocolate) would be *bb ci ci*. Chocolate is one of the commonest types of domesticated mice and since I have used it very extensively in my matings, its relation to the other types may be further stated. It is known that if chocolate is bred to wild gray, and if the gray offspring that are obtained are then inbred, they give, in F_2, the following classes: 9 wild gray, 3 cinnamon, 3 black, 1 chocolate.

It is clear that chocolate is the double recessive type. Of the two genes, that differentiate chocolate from wild gray, chocolate has one in common with cinnamon and the other with black. In other words, chocolate is cinnamon black, and technically should receive this name.

THE EXPERIMENTAL EVIDENCE

Is There a Separate Factor for White-belly?

The first series of experiments was made in order to determine whether the peculiarity of white-belly, shown by the wild race of white-bellied grays, is due to a factor that may be separated from the gray white-bellied mice, or whether it is completely linked to gray (or allelomorphic to it). As wild gray house mice offer some drawbacks in breeding work, I used cinnamon blacks (chocolates). Gray white-bellied mice were bred to

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[2] It is not possible to make a system of allelomorphs (in which the "compounds" are serially epistate to each other) consistent entirely with the system of nomenclature that I have suggested for the usual cases in which mutant allelomorphs are contrasted with the normal allelomorphs of the wild (or supposed original) type.

chocolates.[3] The gray white-bellied offspring were selected and these were bred again to chocolate. The cross, in regard to sex, was made both ways. If there is an independent factor for white-belly that can separate from the factor for gray gray-belly, then some gray gray-bellied mice should appear. None were obtained, as the following table shows. We must conclude either that there is one factor that gives the gray white-bellied coat, or else that the postulated factor for white-belly is so closely linked to the gray factor that it has not separated once in 100 times. Therefore unless such a separation occurs it is simpler to assume one factor for gray white-belly that is allelomorphic to black and to gray gray-belly, etc.

TABLE I

Mating	Gray or Cinnamon White-belly		Black		Chocolate		White	
	♂	♀	♂	♀	♂	♀	♂	♀
Gwb ♀ by Ch ♂....	7	21	2	9	5	11	3	1
Ch ♀ by Gwb ♂....	2	14	3	10	4	10		
Totals..............	9	35	5	19	9	21	3	1

Taking both crosses together, there are 44 grays to 54 blacks and chocolates, which approximate at least to expectation. To these numbers I may add the following data taken from similar experiments made for other purposes in which one parent was, as before, gray white-belly.

Gray-white Belly.		Black or Chocolate.	
♂	♀	♂	♀
17	25	20	20

Presumably, therefore, the results may be treated as though a single gene for gray white-belly exists. It will be observed that the experiment has been made in two ways, for at the time I was aware of the possibility that crossing over, if it occured, might be limited to one sex.

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[3] At the time when the experiment was made all the gray white-bellied mice were heterozygous for black and for agouti (including some with the factor for cinnamon).

We are justified, therefore, in treating gray white-belly as an allelomorph of gray gray-belly, the former dominating. If crossing over should occur, it might perhaps only be realized in the gray or cinnamon mice, since it is possible that the ticked condition of the hair (that is, common to gray and to cinnamon) is necessary to realize this condition. The expected crossover that would be observed would be gray gray-belly mice. The contrary class would then be black or chocolate mice that carry the factor for white-belly that might or might not show the influence of the supposedly separable factor.

My white-bellied stock of mice had been killed after my earlier results had been published, but Mr. B. B. Horton had kept some of my original stock alive, and from him I obtained a few of these mice in 1912 to carry on the above experiments.

An extraordinary sex ratio appears in the next to the last table, where there were 26 males to 76 females, approximately 1:3. The mice were entered when about three weeks old. The sex was noted, but no special attention given to the determination. There is some chance of mistaking the sex of young mice, but one familiar with these animals can determine with certainty the sex at three weeks if sufficient care is taken. I have no reason to suppose that I made such errors which would have to be frequent to give these results. If taken, then, at their face value, the data seem to show that there is a sex-linked lethal gene present here. It is not linked to any of the factors involved, and this is not expected, since neither black nor agouti is sex-linked. If further work confirms this conclusion (and I hold it as a provisional conclusion until it can be further studied) we have here the first evidence of a sex-linked gene in mice. A sex-linked lethal should give a sex ratio of 1♂:2♀.

THE ALLELOMORPHISM OF YELLOW, GRAY AND BLACK

The allelomorphism or "repulsion" of yellow and agouti (gray) may be tested in various ways. One of the simplest tests is the following: Yellows were bred to chocolates. The combination gave yellow and agouti offspring, when certain yellows are used, and yellow and chocolate offspring when other yellows are used. Mixed litters of yellow, agouti and chocolate do not appear. Now when yellow and agouti appear in a given litter (as above) the yellow parent must have carried agouti. If her yellow gene "repels" the agouti gene, then none of the yellow daughters should contain agouti genes, consequently if such yellows are next bred to chocolate the offspring should be only yellow and chocolate (or black) and never yellow and agouti. This, in fact, is what my experiments have shown. In the two following tables the results of crossing yellows by chocolates are given by litters. The yellows that were used at first were for the most part heterozygous for gray white-belly, hence in the earlier litters yellows and grays were generally obtained. The yellow offspring of these earlier litters were for the most part used in the later experiments, hence the later litters are made up of yellows and chocolates. The records (not given here) showed in every case that yellow mice from litters of yellow and gray gave, when bred to chocolate, only yellows and chocolates.

TABLE II

YELLOW ♂ BY CHOCOLATE ♀

LITTERS

Yellow	1	1	1	4	3	1	3	2	4	4	9[4]	4	4	2	5	5	4	3	5	7	2	2	2	2	3	4	3	2	4	1	2	2	2
Gray	.	2	.	5	4	2	2	.	.	4	4	5	5	.	.	3	4	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
Chocolate	.	.	1	.	.	.	.	.	4	.	..	.	.	4	.	.	.	2	3	4	3	.	3	3	.	2	3	2	.	3	4	2	3
White	1	.	.	.	.	.	.	2	.	.	..	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE III

YELLOW ♀ BY CHOCOLATE ♂

LITTERS

Yellow	4	1	4	4	3	4	4	2	4	1	4	8	8	1	2	2	8	3	2	2	1	1	4	3	4
Gray	5	..	2	5	2	1	1	2	..	3	5	1	3	1	..	..	3	..	..	..	..	..	..	..	..
Chocolate	..	..	..	..	..	..	..	..	1	..	..	..	..	..	2	2	..	1	..	2	3	4	2	3	1
Black	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
White	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..

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[4] Probably two litters combined.

TABLE IV

SUMMARY OF LITTERS

Yellow and Gray		Yellow and Chocolate	
Yel.	Gray	Yel.	Choc.
101	78	70	67

The experiment is not demonstrative, however, unless both the yellow daughters and sons are bred to chocolate, for it might be that yellow and agouti are linked and crossing over might occur in one sex and not in the other sex. For instance, if we start again with yellow by chocolate, then if their yellow offspring contain agouti linked to yellow that does not cross over in one sex, let us say in the males, it follows that a yellow male bred to chocolate would give only yellows and chocolates, for the agouti gene would go with the yellow. Therefore, both sexes must be tested. This essential element in the proof has been overlooked by Little, for he fails to state whether his test experiments were made with both sexes. In my main experiments I have used yellow sons only, and the tables are based on those data, but in a few cases I have mated the yellow daughters (whose brothers were agouti) also to chocolate and have found that these females give only yellows and chocolates, which shows for both sexes that no crossing over of yellow and agouti occurs.

A specific case will illustrate this point. A yellow male was bred to a chocolate female and gave 5 yellow and 7 gray offspring in two litters. One of the yellow daughters was bred to chocolate and in four litters produced 11 yellows and 9 chocolates. A yellow granddaughter gave 9 yellows, 7 chocolates and 4 whites.

A yellow female bred to chocolate gave 8 yellows and 16 chocolates, but as I have no record of the preceding generation, I can not be sure that this result is comparable to the last. It shows at least that a yellow female gave only two kinds of offspring.

A "NEW GRAY" FACTOR

A word may be added about the "new gray." In the original stock obtained from Mr. Horton there was a gray female with a not-pure-white belly. She was not used in the main lines of the experiments described above. But she was kept in stock and bred with chocolates. About a year later I noticed in the offspring of a pair of cinnamon white-bellied mice a few mice that looked like chocolates, but which showed, on closer inspection, distinctly ticked hair. One of these new grays bred to black (heterozygous) gave some chocolates, blacks, new grays, and one very dark, almost black, mouse with ticked hair.[5] The female was bred next time to a house mouse (gray gray-belly) and produced all gray gray-bellied offspring that had a dark coat, but not nearly so dark as that present when the new gray is heterozygous for black. Until further tests have been made it can not be stated whether or not the new factor belongs to the yellow-black system of quadruple allelomorphs.

[5] The resemblance of this mouse to the rabbit ''agouti-black'' homozygous for black is very striking (Punnett, *Jour. of Genetics,* II, 1912).